

The University of Chicago

THE DORSAL AXIAL MUSCULATURE OF
CERTAIN PRIMITIVE PERMIAN
TETRAPODS

A PART OF A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE
PHYSICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY

1935

By
EVERETT CLAIRE OLSON

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TWELVE FIGURES

AUTHOR'S ABSTRACT

The development of the dorsal axial musculature is traced from Eryops, through Diadectes, to Dimetrodon. Iguana, a modern form, is used for comparison. The axial muscles of a primitive form, such as Eryops, were thick, fleshy, and metameric; those of more advanced types, such as Dimetrodon, were light, highly tendinous, and largely unsegmented. Diadectes represents an intermediate stage. The changes in the muscles and related changes in the axial skeleton are closely associated with the development of active, terrestrial animals.

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INTRODUCTION

Persistent field work and laboratory research during recent years have made available fairly complete and accurate descriptions of the osteology of many Permo-Carboniferous reptiles and amphibians. Although the majority of workers have concentrated on studies of the skull, enough effort has also been devoted to the post-cranial structure to afford an adequate conception of several key forms. Only a few authors, unfortunately, have made a serious attempt to describe, or to indicate in their figures, muscle scars which often form prominent markings on the bone surfaces.

One factor which has been responsible for this condition is the immature state of comparative myology, since there has been little basis for the interpretation of the muscle scars. A second factor which has hindered the study of the myology of fossil forms has been the incomplete nature of the material available to any one individual. During the last 15 years, however, several excellent papers analyzing the muscle systems of various fossil and recent forms have appeared, although only a few of these have attempted any broad comparisons between groups. Most of the papers have been concerned with the structure of the limbs and girdles, but a few have indicated the arrangement and development of the dorsal axial muscles.

Today, by making use of the material of several collections, by a study of representative modern forms, and by reference to the published data, it is possible to obtain a fairly accurate knowledge of several significant fossil forms and to reconstruct a large part of their musculature. It is the purpose of the present paper to analyze the dorsal axial structure of a series of Permo-Carboniferous animals and to draw certain inferences concerning the evolutionary development of the dorsal axial musculature. Three type genera have been selected for this study, namely: *Eryops*, a large rachitomous amphibian; *Diadectes*, a large American cotylosaur; and *Dimetrodon*, a somewhat specialized pelycosaur. A comparison of myology of these forms indicates in a broad way the significant changes in the stages between the advanced amphibians and the primitive mammal-like reptiles. The axial structure of the recent *Iguana iguana*, a somewhat generalized lacertillian, has been described and figured for comparison with these fossil types.

The methods of study have been much the same as those used by Romer ('22) in his analysis of the locomotor apparatus of certain fossil and recent tetrapods. A comparative study of the axial musculature of modern amphibians and reptiles, made by means of dissections and reference to published descriptions, has furnished the basis for an interpreta-

tion of similar muscles, as indicated by scars of origin and insertion, in fossil types. The majority of the muscles occurring in modern types can be placed quite accurately in fossil forms since the origins and insertions are in analogous positions. The location of certain muscles, notably the smaller muscles of the cervical series, must, however, be inferred from their relations to the other muscles of the group as shown in modern forms. This may be done with considerable confidence, since the study of muscle groups which are well defined in fossil forms has indicated that the musculature has maintained a rather marked degree of stability in the course of evolution.

The character of the muscle scars is of much aid in determining whether the origins and insertions of the muscles were fleshy or tendinous. They fail, however, to give an adequate conception of the fleshy contours. The degree of development of the scars roughly indicates the strength and thus the size of the muscles, and in some cases limits their extent. In general, it is only the interrelationship of all the muscles of any group which afford a conception of an individual muscle.

In order to determine this group relationship, and to attain essentially proper proportions in the drawings, models were constructed with the fossil bone as a base. The muscles were restored in plastic clay. Those which could be placed with reasonable certainty were mounted in appropriate positions, and the more obscure ones were inserted in the series. It was possible in this way to obtain a clear picture of the muscles as they existed in fossil forms. The ventral axial musculature has been restored in the drawings in some cases and its position has been indicated in others.

The illustrations of the bones are almost without exception composites, since a more comprehensive picture can invariably be obtained from several specimens than from one which is apt to lack certain features due to breakage, crushing, or immaturity of the specimen at the time of death. In this regard, specific differences have been ignored since the study is morphological rather than taxonomic.

The terminology applied to the muscles follows, for the most part, that used in a paper on the trunk musculature of a series of living amphibians, reptiles, and mammals by Nishi ('16). Since his work offers the most complete account and comparison of the back musculature yet published, the use of his terminology in the present paper facilitates comparisons of ancient and recent forms. Synonyms which are in common use have also been included.

The materials used in the research were mainly from the Walker Museum of The University of Chicago, the American Museum of Natural History, and the Museum of Comparative Zoölogy of Harvard University. I wish to express my gratitude to Dr. W. K. Gregory of the American Museum of Natural History, to Dr. A. S. Romer of the Museum of Comparative Zoölogy, and to Mr. K. Schmidt of the Field Museum of Natural History for loans of specimens which were of great value. I also wish to acknowledge the assistance of Doctor Romer in the preparation of the paper and of Mr. G. C. Olson in the preparation of the figures.

MYOLOGY

The dorsal axial musculature of the reptiles and the rachitinous amphibians may be divided into four groups: 1) long median, 2) long lateral, 3) short intervertebral, and 4) occipital. These are treated in this order in the following discussion along with certain closely associated hypaxial muscles.

Long median muscles

1. M. spinalis dorsi
2. M. semispinalis dorsi
3. M. spinalis capitis (spinalis parietalis)
4. M. semispinalis cervicis
5. M. extensor caudae medialis
6. M. spinalis cervicis

Definition. This group of muscles, which is continuous from the posterior of the skull to the tip of the tail in reptiles

ABBREVIATIONS USED IN FIGURES

ACET., acetabulum	lig.il.-sac.ext., external ilio-sacral ligament
ad., M. adductor	lig.il.-sac.int., internal ilio-sacral ligament
amb., M. ambiens	lig.int.d., dorsal intermuscular ligament (septum)
ART., articular	lig.int.vert., intervertebral ligament
art.par., M. articulo-parietalis	lig.nu., nuchal ligament
BO., basioccipital	obl.cap.inf., M. obliquus capitis inferior
CA., capitulum	obl.cap.mag., M. obliquus capitis magnus
CER., cervical vertebra	obl.cap.sup., M. obliquus capitis superior
cf., M. coxeygeo-femoralis	OP., opisthotic
D., dentary	P., pubis
D.VERT., dorsal vertebra	PA., parietal
DSO., dermosupraoccipital	PF., postfrontal
ecl., M. extensor caudae lateralis	pipe., M. pubo-ischio-femoralis externus
eem., M. extensor caudae medialis	pifi., M. pubo-ischio-femoralis internus
EO., exoccipital	pt., M. pubo-tibialis
ext.int.c., MM. external intercostals	PTD., pterygoid
ext.obl., M. external oblique	QJ., quadratojugal
fl., MM. flexors	ql., M. quadratus lumborum
F.OBT., obturator foramen	QU., quadrate
IL., ilium	rep., M. rectus capitis posterior
il.c., M. ilio-costalis	repp., M. rectus capitis posterior profundus
il.c.cap., M. ilio-costalis capitis	reps., M. rectus capitis posterior superficialis
il.c.cer., M. ilio-costalis cervicis	S., stapes
il.c.cer.cap., M. ilio-costalis cervico-capitis	SA., surangular
il.c.d., M. ilio-costalis dorsi	semisp.cer., M. semispinalis cervicis
il.ca., M. ilio-caudalis	semisp.d., M. semispinalis dorsi
il.fb., M. ilio-fibularis	ser.ant., M. serratus anterior
il.fem., M. ilio-femoralis	SO., supraoccipital
int.art., M. interarticularis	sp.cap., M. spinalis capitis
int.arc., M. interarcuales	sp.cer., M. spinalis cervicis
int.int.c., MM. internal intercostals	sp.d., M. spinalis dorsi
int.sp., M. interspinalis	SPL., splenial
int.tr., MM. intertransversarii	SQ., squamosal
IS., ischium	S.R., sacral rib
is.tr., M. ischio-trochantericus	T., tabular
J., jugal	TEMP.FOSSA, temporal fossa
l., M. longissimus	tr., M. transversalis
l.cer., M. longissimus cervicis	tr.cap., M. transversalis capitis
l.cer.cap., M. longissimus cervico-capitis	tr.cer., M. transversalis cervicis
l.d., M. longissimus dorsi	TUB., tuberculum
long.colli, M. longus colli	
lev.cos., M. levator costae	
lev.scap., M. levator scapulae	
lig.il.-isch., ilio-ischial ligament	
lig.il.-pub., ilio-pubic ligament	

and presumably in certain fossil amphibians, is bounded medially by the vertebral spines and laterally by the dorsal intermuscular septum which separates it from the long lateral

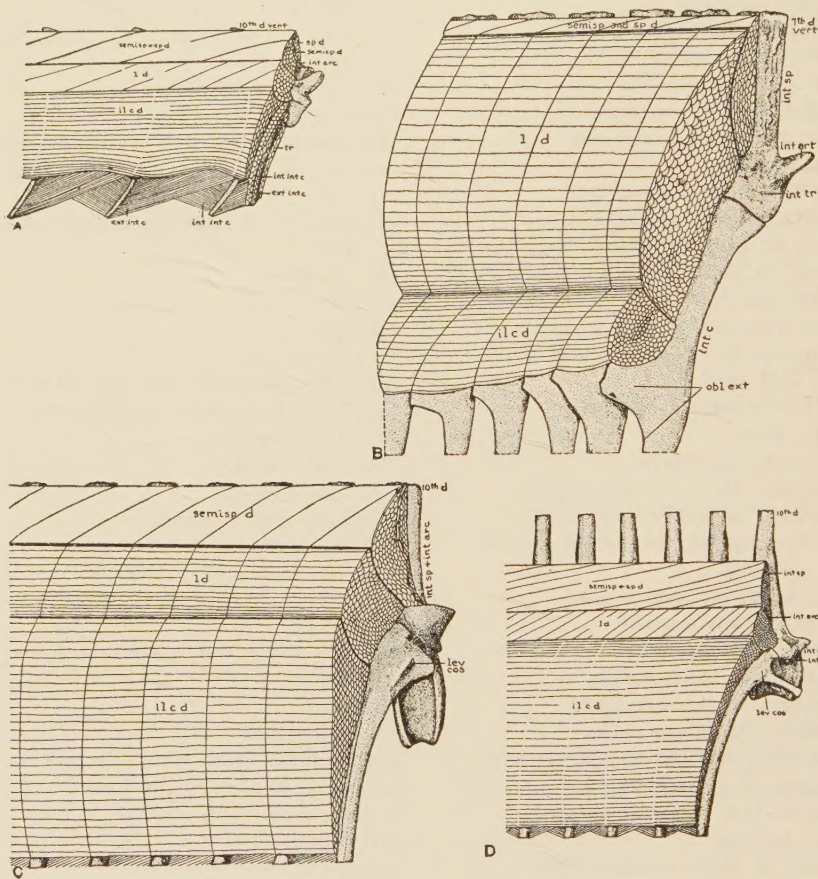


Fig.1 Right aspect of the dorsal axial musculature of types. Anterior ends of muscles cut to show cross sections. A, *Iguana iguana*; B, *Eryops*; C, *Diadectes*; D, *Dimetrodon*.

muscles. The origins are on the spines of the vertebrae and the adjacent neural arches and the insertions are on the neural arches, the dorsal intermuscular septum, and the dorsal part of the posterior of the skull.

In all recent and fossil reptiles, with the exception of a few which are highly specialized or degenerate, the semispinalis and spinalis dorsi compose the dorso-lumbar divisions of the group and the spinalis capitis forms the cervical part along with the spinalis and semispinalis cervicis. Posteriorly the extensor caudae medialis forms the caudal extension of the group. In modern amphibians, however, the situation is radically different. The epaxial musculature of the Urodela is composed of a single muscle which extends from the skull, on which it inserts in three more or less distinct heads, to the tip of the tail. It is divided into segments by myocommata between which fleshy fibers pass. In the Anura, there are either two or three divisions of the group (Noble, '31). The most medial of these, the dorsalis trunci (longissimus dorsi) (Ecker, 1889), is universally developed. Posterior to this is the coccygeo-sacralis (coccygeo-iliacus) (Kingsley, '07 b) which is invariably present. In certain more advanced groups a lateral muscle, the ilio-lumbaris, has developed. The dorsal axial musculature of the caecilians is composed of a long dorsalis trunci divided into a superficial sheet and a deep rounded portion (Nishi, '16).

Condition in types. The median long epaxial muscles of *Iguana iguana* (figs. 1 A, 2 A-D, 4 A) represent the general condition in modern lacertilians. The semispinalis and spinalis dorsi are distinct but intergrown. The spinalis dorsi is composed of slender tendons which pass from the base of the spines over four vertebrae to insert on the spine of the fifth. Superficial tendons of the semispinalis dorsi take origin as a continuation of the tendons of the spinalis dorsi and pass into the fleshy part of the muscle. The insertion of the semispinalis dorsi is by means of tendons passing to the dorsal intermuscular septum.

The spinalis capitis is completely composed of tendons at its origin on the four anterior dorsal and the cervical vertebrae, but is fleshy at its insertion on the posterior surface of the parietal. The anterior part of the muscle is intergrown with the more lateral articulo-parietalis. Near the anterior

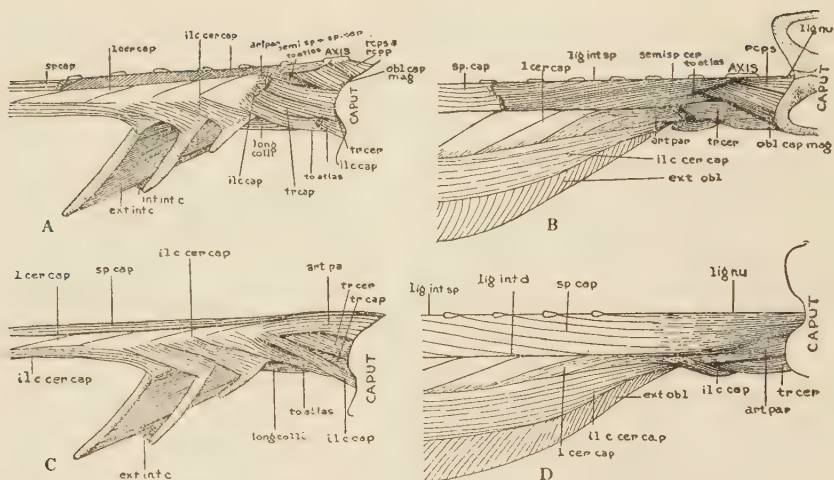


Fig. 2 Lateral and dorsal aspects of anterior dorsal and cervical muscles of *Iguana iguana*. Dorsal fascia and shoulder girdle and associated muscles and ligaments removed in all. A, Lateral aspect. External oblique removed; articular-parietalis, ilio-costalis capituli, and spinalis capituli partially removed. B, Dorsal aspect. Articular-parietalis, ilio-costalis capituli and cervicis, and spinalis capituli partially removed. C, Lateral aspect. D, Dorsal aspect.

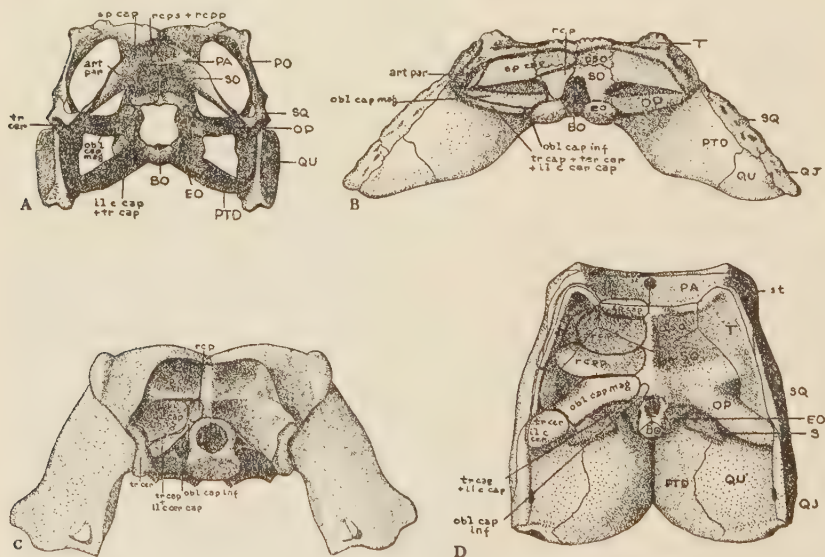


Fig. 3 Posterior aspect of skulls of types. Origins and insertions of muscles indicated. A, *Iguana iguana*; B, *Eryops*; C, *Diadectes*; D, *Dimetrodon*.

end a small fasciculus separates out and runs ventrally to insert at the junction of the parietal and the supraoccipital. The spinalis and semispinalis cervicis are not differentiated in *Iguana*. A single muscle runs forward to insert on a process on the spine of the axis and on the postzygapophysis of the atlas.

Just anterior to the sacrum, a strong tendon passes from the semispinalis dorsi to the posterior tip of the ilium. Posterior to this the group passes into the extensor caudae medialis with no break or abrupt change in character. The superficial tendinous character of this muscle dwindles rapidly and becomes indistinct at the level of the sixth caudal

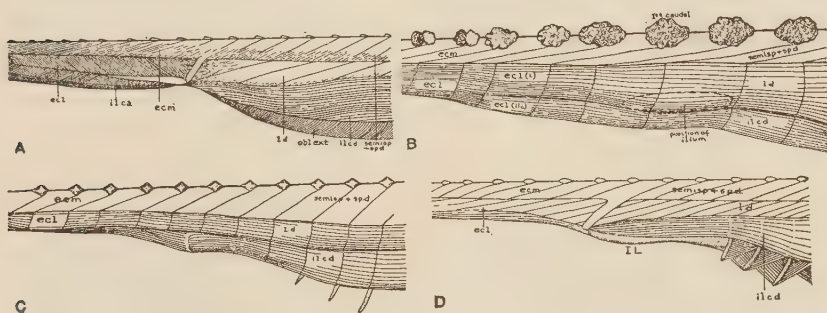


Fig. 4 Dorsal aspect of caudal muscles of types. Fascia and limb muscles and ligaments removed. A, *Iguana iguana*; B, *Eryops*; C, *Diadectes*; D, *Dimetrodon*.

spine. The deep tendons of the spinalis part of the muscle remain distinct to about the fifteenth caudal. Posterior to this, the two sections of the muscle are intergrown and near the tip of the tail are indistinguishable from the extensor caudae lateralis.

The median dorsal muscles of *Eryops* (figs. 1 B, 5 A-D, 4 B), in contrast to those of modern amphibians, appear to have been distinctly separate from the lateral group, a definite break in the continuity of the muscle scars often being apparent on the arches of the vertebrae. There is no indication, however, that the spinalis and semispinalis were differentiated except in the cervical region where a portion of the common muscle appears to have formed the spinalis capitis.

strongly developed ridge on the dermosupraoccipital of the skull by means of tendons and fibers. Ventral to this another division of the muscle passed forward from an indefinite fleshy origin to form the equivalent of the semispinalis and spinalis cervicis of higher forms. This muscle, which appears to have lost contact with the ribs at about the level of the fourth cervical vertebra, inserted on the rugose, caudo-lateral surfaces of the second and third vertebrae by means of strong tendons and on a process of the axial spine in common with the longissimus cervicis.

Posteriorly, the medial epaxial muscle passed without an evident break over the sacral region into the tail to form the extensor caudae medialis. The origins and insertions of this muscle are shown to be similar to those of the dorso-lumbar equivalent by a similar vertebral structure. The texture of the surface of the vertebrae indicates that the tendinous character was preserved in the anterior part of the tail, but probably became obscure posteriorly where the division of the extensor caudae medialis and extensor caudae lateralis becomes indistinct.

The condition of the medial epaxial muscles in the stem reptiles, represented in this study by *Diadectes* (figs. 1 C, 4 C, 6 A-D) was somewhat advanced over that of *Eryops*, for the semispinalis and spinalis dorsi appear to have been distinct muscles with individual origins and insertions. The latter was composed of a series of strong tendons taking origin from highly rugose areas on the dorsal surfaces of the neural arches just anterior to the base of the spines and inserting on the rough, caudo-lateral surface of the spine of the next anterior vertebra. The muscle presumably formed an exceedingly strong support of the axial column resisting both vertical and tensional stresses. It appears to have been most highly developed in the anterior part of the column where the neural spines are short. It was less important in the posterior part where the spines are longer and the function of support was taken over in part by the interspinal muscles. In this region the areas of origin and insertion are

rarely recorded on the bone. Lateral to the spinalis dorsi lay the semispinalis dorsi. This muscle appears to have been composed of short fibers running between the myocommata which were similar to those of *Eryops*, passing from the lateral crests of the spines of the vertebrae to the neural arches. In addition, however, it had a series of origins on

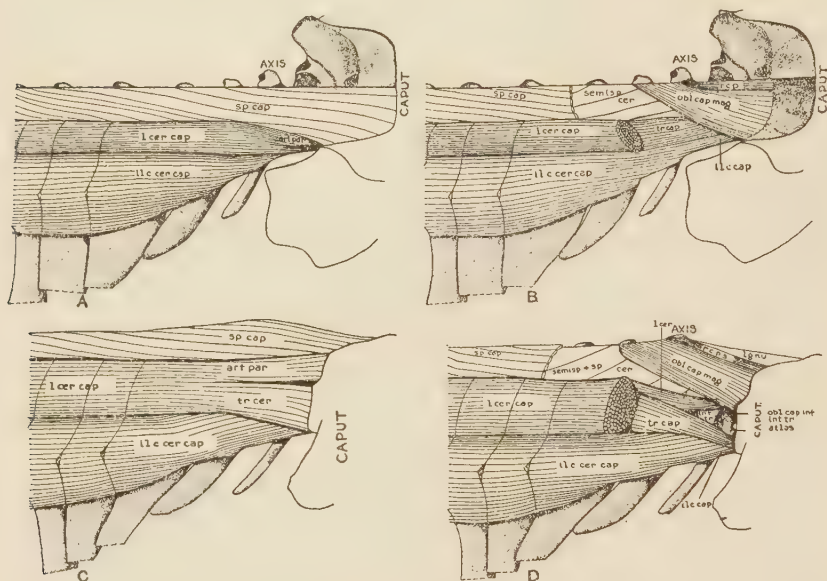


Fig. 6 Dorsal and lateral aspects of inferred anterior dorsal and cervical muscles of *Diadectes*. Dorsal fascia, shoulder girdle and associated muscles, external oblique, and intercostals removed in all. A, Dorsal aspect. B, dorsal aspect. Spinalis capitis and articulo-parietalis partially removed. C, Lateral aspect. D, Dorsal aspect. Spinalis capitis and articulo-parietalis partially removed.

the broad surfaces of the neural arches where tendons seem to have passed into the fleshy part of the muscle from numerous small processes.

At about the level of the seventh vertebra, the semi-tendinous spinalis capitis apparently took origin from tendons of the spinalis dorsi. It passed forward receiving additional tendons from all the rugose dorsal margins of the cervical vertebrae except the first, those of the second and

third being very strong, and inserted in a depression on the posterior margin of the parietal, the anterior part of the dermosupraoccipital, and the inner margin of the tabular on the posterior part of the skull. Anterior to the axis, the median line of this muscle was marked by a very strong nuchal ligament which passed from the knife-like anterior margin of the axial spine to a strong ridge on the midline of the posterior of the skull.

Ventral and medial to the *spinalis capitis*, the intergrown or undifferentiated *semispinalis* and *spinalis cervicis* passed forward from their origins on pitted areas at the base of the neural spines to insertions on the ridges on the posterior margins of the axis and the third cervical vertebra and presumably on the tip of the spine of the axis above the post-zygapophyses. The insertions on the second and third cervicals were very strong. The function of the muscles appears to have been to oppose the action of the strong occipital muscles which originated on these vertebrae.

Posteriorly, the *semispinalis* and *spinalis dorsi* passed with no apparent break into the caudal region to form the strong extensor caudae medialis. The differentiation of the *spinalis* and *semispinalis* was probably not pronounced in the caudal region for it had decreased markedly even in the posterior part of the trunk. The indications are that the extensor caudae medialis was a single segmented muscle comparable to the median trunk muscle of *Eryops*, but the evidence is not conclusive. The rugose spines of the vertebrae suggest that the tendinous character of this muscle was preserved for some distance posteriorly. However, in the posterior part of the tail, the extensor caudae medialis was very likely intergrown with the lateral extensors as in many recent forms.

The medial epaxial musculature of *Dimetrodon* (figs. 1 D, 4 D, 7 A-D) was considerably more advanced toward the condition found in *Iguana*. A noteworthy feature was that the vertical extent of the muscles appears to have been several times the width, in contrast to *Diadectes* in which the

The superficial tendons of the semispinalis dorsi presumably took origin, as in modern forms, at the point of insertion of the spinalis dorsi, as a continuation of the latter. They appear to have passed caudally to lose their identity in the fleshy part of the muscle since no indication of their insertion can be found.

The spinalis capitis probably arose at the level of the seventh or eighth vertebra, taking origin by means of tendons from the somewhat rugose tip of the lower part of the spine of each cervical vertebra except the atlas. It passed forward, widening very little, to insert on a ridge on the parietal and dermosupraoccipital bones of the skull comparable to that found in certain large modern types. The insertion indicates that this muscle was not as strongly developed as the corresponding muscle in *Diadectes*. However, medial to it, as in *Diadectes*, a very strong nuchal ligament ran from the trough-like anterior margin of the spine of the axis to a ridge on the midline of the posterior of the skull much as in modern reptiles.

Underlying the spinalis capitis were the strong, tendinous semispinalis cervicis and the fleshy spinalis cervicis which seem to have taken origin from the bases of the vertebral spines and to have run forward to insert strongly on the lateral ridge of the axis and weakly on a small process of the postzygapophysis of the atlas. An especially strong tendon must have inserted on the prominent dorso-posterior process of the axis.

The semispinalis and spinalis apparently passed without and break into the tail where they formed two parts of the extensor caudae medialis. The markings of the vertebrae in this region indicate that this muscle was similar to the dorso-lumbar part for the first eight or ten caudals. On the remaining vertebra the two parts probably lost their identity and became more fleshy.

Phylogeny of the long median group. Primitively, as indicated in the fossils described above, the origins and insertions of these muscles, which were undifferentiated, seem to have

been accomplished by a series of tendinous myocommata which extended vertically for the whole length of the vertebral spines. These tendinous septa probably divided the muscle group into a series of metameres equal in number to the dorsal and lumbar vertebrae. The same condition seems to have existed in the tail where it persisted in primitive reptiles even after changes had taken place in the dorso-lumbar region. In the course of evolution, a series of strong tendons appears to have developed, passing from pitted areas on the bases of the spines and the adjacent neural arches of the dorsal vertebrae to the posterior lateral surface of the vertebra next anterior. At this stage the more lateral part of the muscle, the semispinalis dorsi, was quite certainly still segmented. In more advanced forms the tendinous origins of the semispinalis dorsi seem to have shifted dorsally to occupy only the tips of the neural spines and the tendons passed more posteriorly as in modern forms. The primitive deep tendons of the spinalis dorsi became restricted in this stage of development to the anterior part of the column, where they had always been most highly developed. A new series of tendons arose, perhaps by a fusion of the shorter tendons between the vertebra, and extended from the bases of the spines to the tips of the more posterior spines where they were continuous with the tendons of the semispinalis dorsi. This gave rise to the typical spinalis dorsi as developed in modern lacertilians. *Diadectes* represents an intermediate stage in this series, while *Dimetrodon* appears to have been essentially the same as modern forms.

In conjunction with this change, more active terrestrial forms seem to have developed. The primitive function of this group of muscles must have been one of support of the vertebral column. But in more advanced forms, where a closer articulation of the vertebrae and a general lightening of the skeletal structure reduced this need, the muscles became flexors of the body, developing a series of intergrown tendons and fibers. Along with this change, the muscle mass became higher and narrower reaching an extreme in such forms as *Dimetrodon*.

The spinalis capitis appears to have been well differentiated in the advanced amphibians such as Eryops and to have changed little in the course of evolution. The bones on which this muscle inserted on the posterior of the skull have changed their position in some forms and have been lost in others. The muscle seems to have inserted on essentially similar areas from primitive to recent forms, and consequently has changed from its primitive insertion on the dermosupraoccipital to its present insertion on the parietal. This, however, is of little significance in the evolution of the muscle, since it is the area of insertion and not the particular bone on which the muscle inserts which is important.

It is significant that in the cervical region where there is need of support because of the weaker articulations between certain specialized vertebrae, because of the heavy skull and the pull of the occipital muscles, the semispinalis and spinalis have retained, even in advanced forms, the primitive function of support indicated in the dorsal region of Diadectes. These muscles seem to have changed very little in origin and insertion or in function from the most primitive reptiles to living forms.

Long lateral muscles

1. M. longissimus dorsi
2. M. longissimus cervico-capitis
 - a. M. articulo-parietalis (complexus major)
 - b. M. transversalis cervicis (complexus minor)
 - c. M. transversalis capitis (spinalis colli)
 - d. M. longissimus cervicis
3. M. ilio-costalis dorsi (sacro-lumbaris)
4. M. ilio-costalis cervico-capitis
 - a. M. ilio-costalis cervicis
 - b. M. ilio-costalis capitis
5. M. extensor caudae lateralis

Definition. The lateral group of long epaxial muscles comprises a series bounded medially in recent reptiles, and apparently in most fossil reptiles and advanced fossil amphibians,

by the dorsal intermuscular septum which separates it from the median group of long muscles. Laterally it may be bounded by uncinata processes on the ribs as in *Sphenodon* or by a complex series of tendinous slips from the external oblique (Maurer, 1899). In many forms, however, this margin is free, the intercostals passing beneath the ilio-costalis and the external oblique passing over it to take origin on the dorso-lumbar fascia.

The median muscle of this group, the longissimus, is continuous for the length of the column. The lateral one, the ilio-costalis, is usually interrupted by the ilium and is sometimes not continuous into the cervical region.

The origins of the group are from the ilium, the transverse processes of the vertebrae, and the dorsal intermuscular septum. The insertions are on the dorsal margins of the ribs, the atlas, and various areas on the posterior part of the skull.

Condition in types. The longissimus dorsi of *Iguana iguana* (figs. 1 A, 2 A-D) is a slender muscle of crescentic cross section which has its origins on the dorsal and inner surfaces of the ilium, the sacral ribs, the prezygapophyses of the dorso-lumbar vertebrae, and the dorsal intermuscular septum. It inserts on the proximal part of the ribs by means of tendons which are continuous with those of the more lateral ilio-costalis dorsi, and on the transverse processes of the vertebrae. The muscle is not segmented but is composed of a number of muscle bundles originating in the tendons from the dorsal intermuscular septum.

The longissimus dorsi passes without a break into the longissimus cervico-capitis (figs. 1 A, 2 A-D). There are four divisions of the latter. The articulo-parietalis inserts on the parietal lateral to the spinalis capitis with which it is intergrown near the insertion. Nishi ('16) has distinguished two divisions of the articulo-parietalis in the Varanidae, a lateral part, the complexus major, and a medial part, the biventer cervicis. No such division is present in *Iguana*. The transversalis cervicis, which lies ventral and lateral to the articulo-parietalis, inserts on the ventral margin of the opisthotic as

a broad but thin muscle. The transversalis capitis passed medially to insert with the most anterior part of the ilio-costalis cervico-capitis on the basioccipital. The longissimus cervicis, the smallest muscle of the series, passes forward under the occipital muscles to insert on the lower part of the arch of the atlas with the most medial branch of the ilio-costalis cervico-capitis.

The ilio-costalis dorsi (figs. 1 A, 2 A-D) is a broad sheet of muscle in Iguana, taking origin from the dorsal and inner surfaces of the ilium and from small tendons from the longissimus dorsi. It inserts on the dorsal margins of the ribs by means of thin tendons. Although these give the ventral surface of the muscle a metameric aspect, they do not appear on the dorsal surface. In the lumbar region, the ilio-costalis dorsi forms a somewhat thickened sheet which is partially intergrown with the longissimus dorsi.

The ilio-costalis cervico-capitis (fig. 2 A-D) is distinctly separated from the ilio-costalis dorsi. It takes origin in five more or less distinct lobes from the dorso-lumbar fascia and the surface of the longissimus. The most posterior of the lobes is rather indistinct at its origin. It inserts on the rib of the fifth cervical vertebra. The fourth takes origin from the surface of the longissimus and the dorso-lumbar fascia along with the third and inserts on the rib of the fourth vertebra. The third inserts on the next anterior rib. The second slip takes origin from the surface of the longissimus and curves ventrally under this muscle to insert on the ventro-lateral surface of the arch of the atlas. The most anterior one has a similar origin, but it passes forward with the most ventral part of the longissimus cervico-capitis to a fleshy insertion on the basioccipital.

The extensor caudae lateralis (fig. 4 A) is divided into two distinct parts in Iguana iguana by a strong tendon originating on the posterior tip of the ilium. This tendon is present on the surface of the muscle to the level of the sixth caudal vertebra where it disappears from sight. However, it is continued as a deep, broad septum which separates the two parts of the

muscle nearly to the end of the tail. The medial part of the muscle is a fairly direct continuation of the longissimus dorsi. It takes origin from the sacral ribs and the strong dividing tendon. It inserts on the prezygapophyses of the caudal vertebrae. The muscle fibers of this portion run antero-dorsally. The lateral division continues posteriorly from the ilio-costalis dorsi, but it is partially separated from it by the ilium. It inserts on the fixed caudal ribs. The fibers of this part run antero-ventrally.

The longissimus in Eryops is shown to have been differentiated from the most lateral ilio-costalis in the dorsal, cervical, and sacral regions by a definite separation of the processes of insertion and the two muscles on the dorsal margins of the ribs.

The longissimus dorsi of this form (figs. 1 B, 5 A-D) quite certainly took origin on the slightly shelved dorsal surface of the ilium, on the sacral rib, and presumably on the dorsal intermuscular septum. It inserted on the strong, serrate crests of the dorsal margins of the ribs by means of tendons which divided the muscle into segments much as in modern amphibians. This muscle was the broadest, and probably the thickest, in the dorsal axial series of Eryops.

At the level of the fifth or sixth vertebra the longissimus dorsi appears to have passed into the longissimus cervico-capitis (fig. 5 A-D) without a break. Somewhere in the region of the fourth vertebra the latter must have become divided into three distinct parts, since there are indications of three areas of insertion on the skull which must be related to this muscle by analogy with modern forms. The most dorsal part of the muscle, which presumably corresponded to the reptilian articulo-parietalis, ran forward to insert on the dermosupra-occipital and the adjacent tabular just lateral to the insertion of the spinalis capitis. The smooth character of this area indicates that the muscle was fleshy. The most ventral of the three divisions, equivalent to the transversalis cervicis and transversalis capitis of reptiles, appears to have originated from the crests of the cervical ribs and to have inserted on the

broad opisthotic and the exoccipital just below the insertion of the obliquus capitis magnus. The third division must have lain between the other two at its origin. It appears to have passed forward under the occipital muscles to insert on the rugose tip of the atlas as in modern reptiles. The strong insertion at this point indicates that the muscle was large and powerful in *Eryops*. It may be called the longissimus cervicis.

The ilio-costalis quite certainly took origin from the outer surface of the ilium and was continuous throughout the length of the column in *Eryops*.

The ilio-costalis dorsi (figs. 1 B, 5 A-D) appears to have passed over the outer surface of the ilium, where it was lightly attached, lying just above the transverse line which marked the dorsal margin of the area of origin of the limb muscles (Romer, '22, p. 559). It inserted on the dorsal crests of the ribs distal to the insertion of the longissimus dorsi and on the proximal part of the large uncinat processes. The very strong insertions indicate that the muscle was segmented by myocommata much as in modern amphibians. The serratus anterior superficialis probably took origin from the tips of the uncinat processes. Lateral and ventral to this muscle lay slips of the external oblique, taking origin from the anterior and posterior surface of the ribs. In the posterior part of the dorsal region, the extent of the insertions shows that the ilio-costalis was quite broad, although never more than half the width of the longissimus dorsi. Anteriorly the muscle appears to have been quite narrow.

The ilio-costalis cervico-capitis (fig. 5 A-D) formed the cranial extension of the ilio-costalis dorsi, inserting in a similar manner to it on the cervical ribs which were well developed in *Eryops*. It was either undifferentiated from or intergrown with the transversalis cervicis and transversalis capitis and must have inserted in common with these two muscles on the opisthotic. This, however, was probably a degenerate condition rather than a primitive character.

The extensor caudae lateralis (fig. 4 B) formed the posterior extension of the longissimus dorsi and the ilio-costalis

dorsi in *Eryops*. The origins presumably were from the sacral rib and the crest of the outer surface of the ilium. There was probably a division for a short distance in the tail. The muscle appears to have been segmented in the anterior part of the tail and probably was in the posterior part as well.

The longissimus of *Diadectes* (figs. 1 C, 6 A-D) was much narrower than that of *Eryops*, the area of insertion on the ribs, which is indicated by a strong serrate ridge being considerably restricted.

The longissimus dorsi (figs. 1 C, 6 A-D) took origin on a depression on the dorsal shelf of the ilium and inserted on the serrate dorsal crests of the ribs and the transverse processes of the vertebrae. It appears to have passed unbroken into the cervical region. It was broad and apparently quite deep, terminating laterally in a series of tendons passing to strong processes at the distal margins of the serrate processes on the ribs. The origin on the ilium was peculiar. On the anterior part of the dorsal shelf of the ilium it undoubtedly lay in the medial deep groove (fig. 10, A and D). But posteriorly it appears to have passed obliquely across the crest of the ilium to occupy the dorsal margin of the inner surface.

The longissimus cervico-capitis of *Diadectes* (fig. 6 A-D) appears to have been divided into four parts as in modern reptiles. The most dorsal of these, the articulo-parietalis, was a thick, fleshy muscle presumably originating from the common longissimus cervico-capitis and the dorsal inter-muscular septum and inserting in a roughly circular depression on the posterior part of the parietal bone of the skull. Ventral to this muscle, the transversalis cervicis passed forward to insert on the strong, caudally directed process of the tabular. Analogy with modern forms indicates that the space medial to this muscle was occupied by a small muscle, the transversalis capitis, which passed ventrally to the opisthotic where it inserted in common with the ilio-costalis capitis just ventral to the insertion of the obliquus

capitis magnus. The fourth division, the most medial muscle of the series, was the longissimus cervicis. It appears to have run medially to an insertion on the lateral surface of the postzygapophysis of the atlas with the semispinalis and spinalis cervicis.

The ilio-costalis dorsi of *Diadectes* (figs. 1 C, 6 A-D) was a broad muscle, presumably thick near the median margins and thin at the lateral extremities. It apparently took origin in the lateral trough on the crest of the ilium, where it was separated from the longissimus dorsi by a ridge of bone (fig. 10, A and D). The insertion of this muscle was by means of strong tendinous leaves to the serrate dorsal crests of the ribs. These tendons must have been quite strong, as the high development of the crests indicates, and most likely passed dorsally through the muscle separating it into a series of metameres.

Anteriorly the ilio-costalis dorsi passed into the ilio-costalis cervico-capitis (fig. 6 A-D). This muscle appears to have had a series of insertions on the serrate dorsal margins of the broad cervical ribs and a strong insertion on the opisthotic of the skull in common with the transversalis capitis. The position of the muscle on the most anterior rib allows no other interpretation of its relations on the skull.

The extensor caudae lateralis of *Diadectes* (fig. 4 C) appears to have been composed of two distinct parts in the anterior portion of the tail, since the vertebrae are similar to those in the trunk region. The median one was a direct continuation of the longissimus dorsi, taking origin on the inner surface of the ilium in common with this muscle and on the sacral ribs. The lateral part quite certainly took origin from the dorso-caudal process of the ilium as it does in all modern reptiles in which this process is developed. These two divisions appear to have inserted on the caudal ribs and the arches of the vertebrae. Posteriorly they probably formed a single muscle as in recent forms. The extensor caudae lateralis appears to have been segmented and probably became intergrown with the medial extensors near the tip of the tail.

The longissimus dorsi of *Dimetrodon* (figs. 1 D, 7 A-D) was a deep but narrow muscle. The similarity between the ilium of this animal and that of *Iguana* suggests that the origin of the longissimus dorsi was much the same in both; that is, from the dorso-posterior tip of the ilium, the sacral ribs, and the dorsal intermuscular septum. It passed forward to definite areas of insertion marked by prominent processes on the proximal margins of the dorsal surfaces of the tubercula of the ribs and on the transverse processes of the vertebrae. Apparently, strong but narrow tendons passed to these areas much as in modern forms. The muscle does not appear to have been segmented.

There was probably no break between the longissimus dorsi and the longissimus cervico-capitis (fig. 7 A-D). The latter appears to have been divided into four distinct members as in *Diadectes*. The articulo-parietalis apparently inserted on a ridge on the caudo-lateral extension of the parietal and the outer margin of the tabular. The transversalis cervicis most likely inserted on the tabular and the lateral part of the opisthotic in common with the ilio-costalis capitis. The more ventral transversalis capitis appears to have passed medially, as in *Iguana*, to insert with a branch of the ilio-costalis cervico-capitis on the exoccipital. The medial longissimus cervicis was a small muscle which must have run under the occipital muscles since its insertion on the transverse process of the atlas is well marked by a small process.

The ilio-costalis dorsi of *Dimetrodon* (figs. 1 D, 7 A-D) was somewhat broader and presumably thinner than that of *Diadectes*. It quite certainly originated on the dorsal and inner surface of the ilium as in *Iguana*. Its insertions are indicated by rather poorly developed processes on the dorsal surfaces of the ribs. The tendons from these processes probably did not pass through the muscle to give it a meta-meric appearance on the dorsal surface since they must have been quite weak. This is the condition which is found in most modern reptiles.

The origin of the ilio-costalis cervico-capitis in *Dimetrodon* (fig. 7 A-D) is somewhat in doubt. In the more primitive forms discussed the muscle appears to have been a direct continuation of the ilio-costalis dorsi since there is no change in the dorsal crests of the ribs. In recent forms in which the cervical ribs are short or absent, the origin is from the dorsal surface of the longissimus and the dorso-lumbar fascia. *Dimetrodon* represents an intermediate stage in skeletal development, its cervical ribs being rather long but directed ventrally to form a rather slender neck. The condition seems to be somewhat closer to that of *Diadectes* than to that of modern forms. The insertions of the muscle indicate that there were probably three divisions. The most lateral one seems to have run forward and inserted in common with the transversalis cervicis on the opisthotic. Medial to this, a smaller portion probably inserted on the exoccipital along with the transversalis capitis. A third division quite certainly passed medially to insert on a rugose area on the transverse process of the atlas.

The extensor caudae medialis of *Dimetrodon* appears to have been composed of two divisions in the anterior part (fig. 4 D). The medial one formed the caudal extension of the longissimus dorsi and presumably took origin from the ilium and sacral ribs in the same manner as in *Iguana*. It undoubtedly inserted on the caudal vertebrae. The lateral part quite surely took origin by means of a strong tendon from the posterior tip of the ilium and inserted on the caudal ribs. Posteriorly, at an undetermined level, the medial and lateral parts probably became intergrown to form a single muscle as in most recent forms.

Phylogeny of the long lateral muscles. Primitively the ilio-costalis seems to have been a narrow band of muscle lying lateral to a broad, thick longissimus. During the course of evolution, the former became a broad but thin sheet and the latter was reduced to a narrow equidimensional band. The changes, although most pronounced in the trunk, also occurred in the caudal and cervical regions.

Romer ('22, pp. 559-560) outlined a series of steps in the development of the epaxial muscles in relation to the evolution of the ilium. Primitively, according to his argument, the blade of the ilium separated the long axial muscles into a medial series passing freely above the ilium and a lateral series with origins and insertions on the outer surface of the ilium. In this stage, represented by *Eryops* and the Urodela,

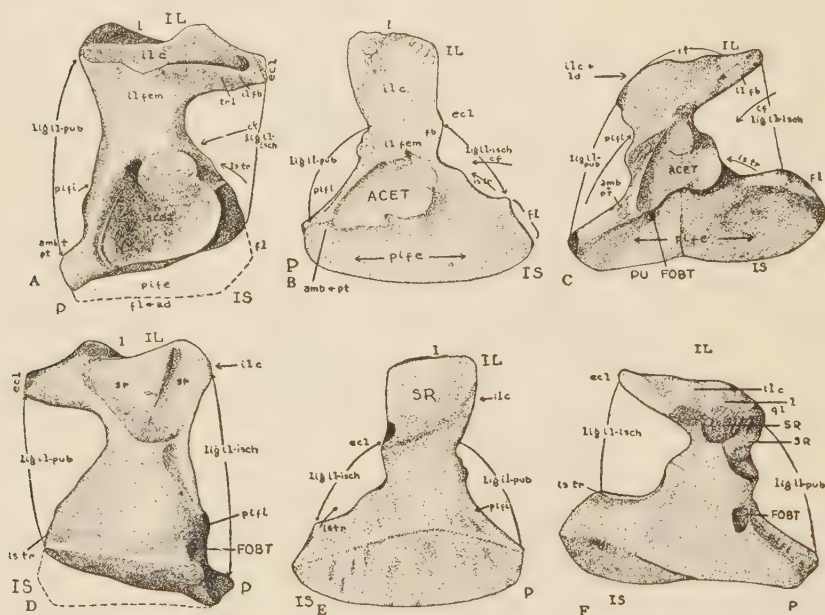


Fig. 10 Innominate of fossil types. Origins and insertions of muscles and ligaments indicated (limb muscles after Romer, '22). A, Diadectes, lateral aspect; B, *Eryops*, lateral aspect; C, *Dimetrodon*, lateral aspect; D, Diadectes, medial aspect; E, *Eryops*, medial aspect; F, *Dimetrodon*, medial aspect.

the limb muscles from the ilium occupied only a small area at the base of the blade. In *Eryops* a transverse line marking the dorsal termination of this area may often be found. In the course of development, this lower area expanded greatly to accommodate the limb muscles which increase markedly in size. As this occurred, the upper part of the lateral surface turned inward carrying with it the axial muscles. Subsequently, a further dorsal expansion of the

ilium took place, leaving the axial muscles on an internal shelf above the sacral ribs.

A careful study of the dorsal axial muscles confirms these conclusions. *Eryops* is considered to represent the primitive stage in which the longissimus took origin on the slightly shelved dorsal crest of the ilium and the sacral ribs, while the ilio-costalis lay ventral to it on the broad outer surface of the ilium (fig. 10 B and E). *Diadectes* appears to be an intermediate form in which a broad dorsal shelf had developed on the ilium for these muscles (fig. 10 A and D). The longissimus occupied the anterior part of the shelf but had been carried to the inner surface posteriorly. The ilio-costalis remained on the shelf for the whole length of the ilium. In *Dimetrodon* (fig. 10 C and F) the ilium has reached an essentially modern development, and both muscles lay medial to the outer blade of the bone taking origin only from the dorsal and inner surfaces by means of tendons.

It seems probable that the differentiation of the ilio-costalis and the longissimus took place as a result of the dorsal growth of the ilium which provided the long lateral muscles with two areas of origin. If this be true, the primitive ilio-costalis must have been narrow and the longissimus broad because of the position of the ilium. This is precisely the condition which is found in *Eryops*. As the dorsal part of the ilium folded inward, the longissimus appears to have been carried with it to the position noted in *Diadectes*. The outer margin of the ilio-costalis, however, has remained almost in the same plane even in forms in which it has been isolated from the exterior of the ilium. It appears to have retained its original insertions on the ribs, but to have increased in width by medial growth, following the longissimus, to produce the condition inferred in *Diadectes*. A continuation of the process gave rise to the type of axial musculature found in *Dimetrodon* and certain recent forms.

An equally interesting, but more obscure, series of changes seems to have taken place in the cervical region. The tendency of the cervical muscles of the lateral series has been to

migrate medially and to produce a relatively slender, flexible neck. Unfortunately it is very difficult to obtain an accurate idea of the very primitive condition since the muscles of *Eryops* had been altered by the depression and broadening of the skull.

In very primitive amphibians the ribs extended from the sacrum to the first vertebra without any great change in length. As more active terrestrial animals developed, the cervical ribs became shorter until in recent forms they are much reduced or absent. Primitively, as indicated in *Eryops*, the ilio-costalis cervico-capitis appears to have been a direct

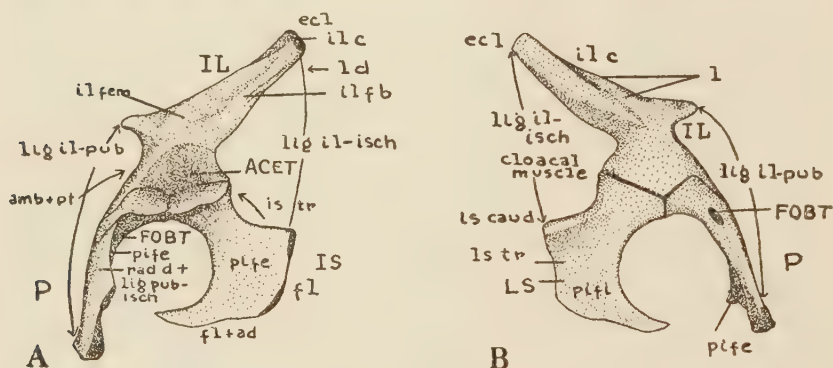


Fig. 11 Innominate of *Iguana iguana*. Origins and insertions of muscles and ligaments indicated. A, Lateral aspect; B, Medial aspect.

continuation of the dorso-lumbar equivalent and to have inserted on all the cervical ribs. As the ribs became shorter and bent ventrally, this muscle seems to have been carried medially. The ilio-costalis appears to have inserted primitively along the whole expanse of the opisthotic as in *Eryops*. In more advanced forms, it seems to have been carried inward to develop a new insertion on the basioccipital. Its primitive insertion on the ribs was shifted to the adjacent vertebrae. A final step in the sequence is seen in modern reptiles, where the muscle has lost its continuity with the ilio-costalis dorsi and takes origin on the surface of the longissimus and the dorsal fascia.

The history of the longissimus cervico-capitis is not so clear. Primitively, it appears to have inserted on the cervical ribs and the lateral part of the skull. As the ribs diminished in length, the ventral part may have been carried medially to the atlas and the basioccipital, while the dorsal part, which was not in contact with the ribs, retained its original insertions on the posterior of the skull.

It has been indicated in the discussion of the long epaxial musculature of the types, that, with the development of more active terrestrial forms, the massive, fleshy muscles were replaced by thin, tendinous ones. As this change occurred the primitive myocommata lost their original positions and became part of a complex series of tendons. This process seems to have occurred first in the most medial muscle of the group and to have progressed laterally. Diadectes probably represents the initial stage in which only the spinalis dorsi had changed. In Dimetrodon the spinalis dorsi and the longissimus dorsi were no longer segmented, and the tendons of the ilio-costalis dorsi probably did not pass through the muscle. The Iguana is in the same stage. An intermediate form is found in the modern Sphenodon in which the semispinalis and spinalis dorsi are composed of a complex series of tendons, but the longissimus dorsi and ilio-costalis dorsi are segmented (Byerly, '26; Nishi, '16, p. 250). Certain modern reptiles such as Varanus and the Ophidia have gone a step farther than Iguana and have lost all signs of segmentation. In these the ilio-costalis dorsi is likewise composed of a complex series of tendons passing through fleshy fibers. This condition is the rule in mammals, but Echidna and Ornithorhynchus have retained the segmentation in all but the most anterior part of the ilio-costalis dorsi (Nishi, '16, Taf. XII, figs. 4-5).

Short segmental muscles

1. MM. interspinalis
2. MM. interarcuales
3. MM. interarticulars

4. MM. intertransversarii (ventral)
5. MM. levator costae (ventral)
6. MM. intercostals (ventral)
 - a. external
 - b. internal

Definition. The short segmental muscles comprise a deep group lying under the long dorsal muscles and often intergrown with them. All the members extend between adjacent vertebrae or ribs, or between vertebrae and ribs.

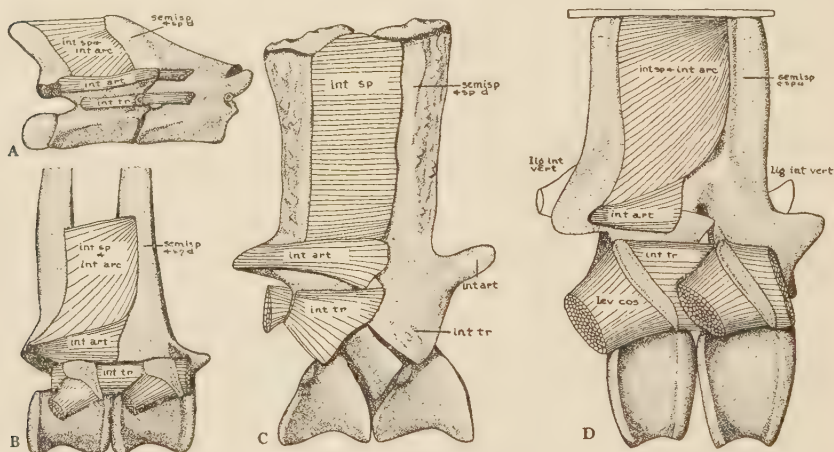


Fig. 12 Short segmental muscles of types. A, *Iguana iguana*; B, *Dimetrodon*; C, *Eryops*; D, *Diadectes*.

Condition in types. The interspinals and interarcuales (fig. 12 A-D) seem to have been very similar in all the type forms. They are so intimately intergrown as to be inseparable in *Iguana*, and apparently in most fossil forms as well. The origins and insertions are on the lateral surfaces of the vertebral spines and the adjacent neural arches. The muscles are generally present from the second cervical vertebra to the posterior caudal region where they are intimately intergrown with the extensor caudae medialis. The ventral margin is marked by the interarticulars and the medial surface is in contact with the interspinal ligament.

In *Iguana iguana* the muscles are thin and semitendinous. They are somewhat intergrown with the *spinalis dorsi*, *spinalis cervicis*, and *extensor caudae medialis*. The neural spines of *Eryops* are heavily marked by ridges and processes which suggests that the interspinals and interarcuales were thick and tendinous. They must have played an important part in the support of a rather weak spinal column. Similarly, in *Diadectes*, they appear to have been very strong, especially in the cervical region where the highly rugose character of the spines indicates that they were tendinous. The condition in *Dimetrodon* was apparently quite similar to that in *Iguana*, but the size of the animal probably required a greater differentiation from the long axial muscles.

The interarticulars (fig. 12 A-D) appear to have been present in all the type forms. They lay just ventral to the interarcuales. The origins were apparently on the lateral surfaces of the postzygapophyses of all the vertebrae and the insertions were on the prezygapophyses of the same vertebrae and the postzygapophyses of the next anterior one, as they are in *Iguana* and other modern reptiles.

In *Iguana* these muscles were thin and much intergrown with the *semispinalis*. In *Eryops* the shape of the arches indicates that the muscles were rather long and narrow. Only rarely is their presence recorded by a scar. In *Diadectes* the interarticulars seem to have been very strong, taking origin, in the dorsal region, by means of a tendon from a triangular pit on the anterior surfaces of the postzygapophyses. In *Dimetrodon* they were probably fairly well developed, but only rarely did they leave any scar on the bone.

The *intertransversarii* (fig. 12 A-D), which are a medial differentiation of the intercostals, have their origins and insertions on the transverse processes of all the vertebrae which bear ribs. Their shape and size is dependent on that of the transverse processes. They are small in *Iguana*, but presumably were large in *Eryops*, *Diadectes*, and *Dimetrodon*. They very seldom leave well-developed scars.

The levator costae (fig. 12 A-D), when present, take origin on the posterior surfaces of the transverse processes of the vertebrae which bear ribs and insert on the anterior surfaces of the heads of the ribs. They are generally quite well developed in large animals, but often are absent in small ones.

In Iguana, the levator costae are present on four or five cervical vertebrae, but are small and indistinct. Prominent raised areas on the heads of the ribs of *Diadectes* and *Dimetrodon* indicate that these muscles were very well developed. In the former they were short and stout and must have played an important part in the support and movement of the ribs. They were long and rather slender in *Dimetrodon*. There is no evidence that the levator costae were developed in *Eryops*.

It is generally impossible to determine the exact pattern of the intercostal muscles in fossil forms. The shape of the ribs often indicates that an external and internal set was present, but shows nothing as to the course of the individual groups. In modern forms there is much variation in these muscles in different animals.

In *Eryops* the intercostals must have been highly specialized, passing, as they did, between the very broad surfaces of the ribs. This must have been the case in the cervical region of *Diadectes* as well.

Phylogeny of the short intervertebral muscles. There is little to be noted about the evolutionary development of these muscles. They seem to have been present in the most primitive forms studied in essentially the same way as they are in modern forms. As the spinal column became stronger and lighter, these muscles seem to have diminished in size. In general, they are adapted to the particular need of the various animals in which they occur.

Occipital muscles

1. *M. rectus capitis posterior*
 - a. *M. rectus capitis posterior superficialis*
 - b. *M. rectus capitis posterior profundus*
2. *M. obliquus capitis magnus*
3. *M. obliquus capitis superior*
4. *M. obliquus capitis inferior*

Definition. The occipital muscles comprise a series of short members passing between the first three cervical vertebrae and the occipital region of the skull. The origins are on the vertebrae and the insertions, on the atlas and the skull. They are present in almost all living reptiles but absent in modern amphibians. They appear to have been present in most fossil reptiles and many fossil amphibians.

Condition in types. Four muscles of this group can be distinguished in *Iguana iguana* (fig. 2 A-B), the obliquus capitis inferior being so intergrown with the obliquus capitis magnus that it cannot be separated. The rectus capitis posterior superficialis and profundus are both present, but they are somewhat intergrown and form a functional unit. They take origin on the dorso-lateral part of the surface of the axial spine and insert on the supraoccipital just below the insertion of the spinalis capitis.

Below and somewhat lateral to these muscles in *Iguana*, the large obliquus capitis magnus passes forward from the lateral surface of the axial spine to insert on the opisthotic just dorsal to the insertion of the transversalis cervicis. The obliquus capitis superior is an exceedingly small, fleshy muscle which takes origin on the ventro-cranial surface of the axial spine and passes to the postzygapophyses of the atlas.

The occipital group of *Eryops* (fig. 5 B and D) was composed of three or possibly four muscles. The most dorsal of these appears to be equivalent to the rectus capitis posterior of reptiles. It took origin in a depressed area on the dorso-cranial margin of the lateral surface of the axial spine, in a position very similar to that of the origin of the same muscle in *Iguana*. It passed forward to insert in a slight

depression on the median dorsal part of the opisthotic and the base of the dermosupraoccipital. In one specimen there are indications that this muscle was divided into two parts at the origin but this cannot be confirmed in any other specimen available. Ventral to this muscle lay a large muscle which was equivalent to the obliquus capitis magnus of reptiles. It took origin on the lateral surface of the axial spine in an area which is well defined in several specimens by the texture of the bone. The insertion of this muscle was apparently on the rough surface of the opisthotic just above the inferred insertion of the longissimus cervico-capitis. The third muscle of the series, equivalent to the rectus capitis superior of reptiles, was very small and its scars of origin and insertion can be located only with difficulty in a few specimens. It appears to have passed forward from the arch of the atlas to an insertion on the opisthotic just medial to the insertion of the obliquus capitis magnus. It is mainly the positions of the other occipital muscles which determine that this muscle was present. There is no evidence that the obliquus capitis inferior was present in *Eryops*. However, since it is generally a small, fleshy muscle, it may have been present and left no evidence on the bone.

The occipital muscles of *Diadectes* (fig. 6 B and D) appear to have been composed of three or possibly four muscles as in *Eryops*. The rectus capitis posterior appears to have been a narrow muscle which took origin from the dorsal part of the lateral surface of the axial spine just below the process from which a tendon of the spinalis capitis arose. It passed forward to insert in a well-defined circular depression on the supraoccipital region of the skull just lateral to a strong ridge which marked the insertion of the nuchal ligament. Lateral and ventral to it lay the large obliquus capitis magnus. This muscle took origin from a poorly defined area on the lateral surface of the axial spine and apparently from the tip of the third cervical vertebra as in *Iguana*. The spine of the third vertebra is quite highly specialized in *Diadectes* and presumably played an important role in the support of

the skull by virtue of the heavy muscles which originated on it. The obliquus capitis magnus inserted in a well-defined circular depression on the supraoccipital region of the skull, apparently on the supraoccipital and opisthotic bones. The sutures on skulls showing this depression cannot be made out. Below it, a very small obliquus capitis superior was probably present, passing between the anterior part of the spine of the atlas and the exoccipital. The insertion on the skull is quite clear, but the position on the axis must be inferred from the condition of modern forms. The obliquus capitis inferior may have been present, but the evidence is not conclusive.

Dimetrodon (fig. 7 B and D) appears to have had four or five separate muscles in the occipital series. The poor preservation of the skulls of this animal has made determinations of the areas of insertion of the occipital muscles very difficult. Most of them have been inferred from comparisons with modern forms. The rectus capitis posterior superficialis and rectus capitis posterior profundus may or may not have been separate muscles. There is some evidence on the skull of two areas of insertion, suggesting that they were separate. The area of origin on the dorso-cranial part of the lateral axial surface is rather poorly defined. The rectus capitis posterior superficialis probably inserted in a slightly depressed area on the supraoccipital, dermosupraoccipital, and tabular bones of the skull. The rectus capitis posterior profundus seems to have passed to an area just below the insertion of the superficial branch on the supraoccipital and tabular. The rectus capitis posterior must have been in contact with the pro-atlas and may have had a secondary origin from it.

The obliquus capitis magnus was the largest muscle of the occipital series in Dimetrodon as it is in Iguana. It quite certainly took origin from the broad lateral surface of the axial spine and inserted on the slightly raised opisthotic. It must have been in contact with the pro-atlas, but there is no evidence that it was attached to it. The most ventral

muscle of the series was the obliquus capitis superior which presumably ran from a small process on the postzygapophyses of the atlas to a rather indefinite insertion on the medial part of the opisthotic and the adjacent exoccipital. Apparently continuous with this muscle on the atlas was the small obliquus capitis inferior. It presumably took origin from the most ventral part of the lateral surface of the axial spine and inserted on the postzygapophysis of the atlas.

Phylogeny of the occipital muscles. The occipital muscles appear to have been well differentiated in forms as primitive as *Eryops*. Only the rectus capitis posterior has undergone much change, enlarging and dividing into two muscles.

However, there have occurred certain changes in the insertions of the occipital muscles and also the cervical muscles of the long axial groups. In *Eryops*, *Seymouria*, and certain other primitive amphibians and reptiles, the upper margin of the area of insertion of these muscles is a straight or slightly curved line from dorsal aspect. In *Eryops*, the area of insertion of the muscles is quite limited and rises in a nearly vertical plane above the occipital condyle. The dermosupraoccipital and the tabulars form the dorsal part of the area. In *Diadectes* the dorsal aspect of the upper margin of the area resembles a 'W' with the base anterior. Both the dermosupraoccipital and the parietals are incorporated into the area. The surface area for muscle insertion is increased and slopes forward from the condyle leaving only the limbs of the 'W' at the level of the occipital condyle. The same condition, even more pronounced, is present in *Dimetrodon*.

These changes were related to several important muscular developments: 1) the distance between the origins on the axis and insertions on the skull was increased and the angle of the occipital muscles to the vertical axial plane decreased; 2) the insertions of the muscles became stronger by virtue of an increased area; 3) the spinalis capitis, rectus capitis posterior, and obliquus capitis magnus gained new insertions on medially directed surfaces; 4) the height of insertion of

the spinalis capitis and rectus capitis posterior above the occipital condyle was increased. All these changes must have tended to produce an increase in the range of movement of the head. Correlated with them is the development of the articulation of the occipital condyle and atlas to permit a greater latitude of movement.

DISCUSSION

Phylogenetic implications. It has been pointed out in the foregoing discussion that the axial muscles of the living reptiles and amphibians are very dissimilar. There is no apparent homology between the divisions of corresponding groups of axial muscles. This suggests that a similar lack of homology might have existed between fossil amphibians and reptiles. If this were true, there could be no justification for establishing, as a basis for the study of muscle development, a series including the type forms employed in the present study. There are, however, lines of evidence which indicate that the Rachitomi, while not actually on the evolutionary line leading to the primitive reptiles, did possess a muscle pattern which was quite similar and presumably homologous to that found in the ancestors of the reptiles, perhaps the Embolomeri.

The dorsal axial musculature of Eryops and Diadectes was apparently similar in general outlines. The points of origin and insertion of the majority of axial muscles of these two forms were located in comparable positions. On the basis of this, which is practically the only criterion of homology applicable in fossil forms, the various individual members of the muscle groups appear to have been homologous. The musculature of Eryops, however, seems to have been more primitive than that of Diadectes, since the muscles were not as highly differentiated as in the latter, and since the trends of development inferred in the reptiles, if carried back, imply the existence in their ancestors of a condition comparable to that found in Eryops. It is the consensus of opinion that the Cotylosauria and Rachitomi developed their characteristics from less specialized common ancestors, presumably

the Embolomeri. An examination of the skeleton of Seymouria, a primitive cotylosaur which was close to the amphibian ancestors, indicates that the axial musculature of this animal was quite similar to that of Diadectes. This evidence, coupled with the apparent homology between the axial musculature of Eryops and Diadectes, strongly suggests that a basic muscle pattern possessing the essential features found in these two forms was present in the common amphibian ancestor. Eryops presumably had not advanced as far from the ancestral condition as had Diadectes. Thus, on rather theoretical grounds, it seems safe to include Eryops as the primitive member of the series from the advanced Paleozoic amphibians to the primitive mammal-like reptiles, in spite of the fact that it was not actually ancestral to the reptiles.

There are two possible explanations of the lack of accordance between the muscles of modern amphibians and the advanced Paleozoic forms. The ancient and modern forms might be related only through some exceedingly primitive ancestor from which they developed along separate evolutionary lines; or, assuming that the known advanced Paleozoic forms were structurally similar to the ancestors of the modern ones, neotony might exist among the latter, inhibiting the development of muscles present in the Paleozoic ancestors. The first possible explanation is difficult to check since the ancestry of neither of the major living groups, the Anura and Urodela, can be traced back into the Paleozoic era. Neotony is evident in the Urodeles, but does not seem to be important in the Anura.

The Anura have been a separate group, possessing most of the specialized characters in existence today, at least since the Jurassic. They must have come from small, normally shaped Paleozoic forms. Presumably they have had a history not closely connected to that of the other groups since late Paleozoic times. That the pattern of the epaxial musculature, which is highly specialized in its divisions although primitive in the retention of myocommata, was derived from

a form which was immediately ancestral to the Rachitomi or the Cotylosauria seems unlikely. The Anura probably represent a group which became independent of the main line of Paleozoic forms very early in the history of the amphibians, before the muscle pattern which has been inferred in the ancestors of the Rachitomi and Cotylosauria had become established.

The Urodela are much more similar in general outlines to the rachitomous and embolomorous amphibians than are the Anura. Fossil representatives may be traced back to the lowest Cretaceous. They possess many features, such as a cartilaginous skeleton, segmental axial muscles, and small limbs, which have been called primitive. These 'primitive' features can be accounted for, in most cases, by degeneracy and neotony. The condition of the epaxial musculature is interesting in light of the larval character of the adults. The single long muscle, which is separated into segments by myocommata, is similar to the embryonic epaxial muscle of more advanced groups. It appears thus to be a neotonic character, one which is retained even in the most advanced forms of the Urodela. Considering this neotony, there appears to be nothing in the axial musculature of the Urodela to indicate that they may not have come from essentially the same ancestors as the rachitomous amphibians.

Adaptive developments of the skeleton and musculature. The development of animals well adapted to a terrestrial existence from sluggish, swamp living, ancestral types has produced a rather striking series of changes in the skeletons and muscles of the forms involved. The most pronounced changes have been in the limbs and girdles. They have been discussed in detail by Romer ('22). He points out that the most important adaptive changes in the limbs have been a relative increase in the length of the limb bones and a rotation of the front and hind limbs so that they lay under the body rather than to the sides as in amphibians and primitive reptiles. Corresponding changes have occurred in the girdles and the muscles of the limbs and girdles.

Although the changes in the axial structure are not so pronounced as in the limbs, certain ones have been important in the development of more active, land living animals (see cited papers of Case, Watson, and Williston).

The most evident change in the axial skeleton of the forms studied is a progressive reduction of the size and weight of the bones. In conjunction with this change, there has been an increase in the supporting strength of the axial structure. This has been accomplished in the spinal column by a loss of the intercentra and a corresponding closer articulation between the pleurocentra, a fusion of certain elements such as the sacral vertebrae, the sacral vertebrae and ribs, and the ribs and the ilium, and, in reptiles, by a proportionate increase in the length of the neural spines to which the interspinal muscle attached. These processes produced interesting results. The skeleton was lightened and rigidity was increased in the dorso-ventral axial plane, permitting the body to be more easily raised off the ground and increasing the opportunity for more rapid locomotion. Flexibility was increased in the horizontal plane by a reduction in the width of the zygapophyses and arches of the vertebrae and a diminution in the size of the ribs, especially in the cervical region.

There was a corresponding development of the axial musculature, tending to produce a dorso-ventral rigidity and a lateral flexibility. The powerful, heavy muscles which appear to have been present in such primitive forms as *Eryops*, altered during evolutionary development into lighter and narrower muscles by a process of medial migration. This migration appears to have been most pronounced in the cervical region where it produced a slender, highly flexible neck. The long epaxial muscles, with the exception of the ilio-costalis, have become much deeper in proportion to their width. Muscles of the shape thus developed are well adapted to resist the pull of gravity and to produce rapid lateral flexions of the vertebral column. The ilio-costalis became a thin sheet of muscle which facilitated a freedom of motion of the ribs but offered little support to the axial system.

In conjunction with this migration, two closely connected changes appear to have taken place in the composition of the muscles, namely, the loss of myocommata and the development of tendons. Muscles such as those in *Eryops* presumably were adapted only to a slow, crawling type of locomotion as found in the Urodela. The loss of the myocommata, which probably have gone to form certain members of the tendon complex, and the development of tendons must have given rise to a series of muscles in which there was close coordination between the parts of a single muscle and between the members of a muscle group. The tendons appear to have developed as a means of support of the axial column. They became closely grouped on either side of the vertebral column and intimately related to the spines and arches of the vertebrae and to the proximal parts of the ribs. In connection with this primitive function of support, it is interesting to note that the tendons seem to have first appeared in the most medial of the long muscles and to have developed subsequently on the more lateral ones. *Diadectes* appears to represent an initial stage in which only the most medial of the muscles was tendinous. No fossil form in which the pattern of the axial muscles has been studied shows the stage in which only the spinalis and semispinalis are tendinous, but this condition is found in *Sphenodon*.

In primitive forms, the tendons appear to have functioned mainly as supports of the axial column. In more advanced forms, where more support was afforded by the specialized vertebrae, the tendons appear to have become adapted to act as flexors along with the more fleshy parts of the muscles. This stage apparently had been reached in *Dimetrodon*, an animal which seems to have been one of the earliest of the large, active carnivores.

SUMMARY

The following are the major points in the development of the dorsal axial structure which have been presented for the first time or for which additional evidence has been cited:

1. The median and lateral groups of long epaxial muscles were apparently separate in the rachitomous amphibians and the most primitive reptiles.

2. The long back muscles primitively were metameric, originating and inserting by means of strong, tendinous myomata. In the course of evolution, this character was lost, first by the most medial muscle and then successively by the more lateral muscles. In modern reptiles, vestiges of the segmentation are often preserved in the ilio-costalis of rather generalized forms.

3. Primitively, the long dorsal axial muscles were thick and fleshy, but in more advanced forms they became thin and tendinous.

4. The spinalis dorsi and semispinalis dorsi appear to have been differentiated in the stem reptiles, but to have formed a single muscle in the rachitomous amphibians.

5. The primitive function of the median back muscles seems to have been one of support. In more active terrestrial forms, these muscles became primarily flexors, only the cervical muscles retaining their original function.

6. The median back muscles of *Dimetrodon* occupied only the lower part of the neural spines. Their dorsal margin was marked by a change in the shape of the spines.

7. The ilio-costalis dorsi and longissimus dorsi were differentiated in all reptiles and in the rachitomous amphibians.

8. The differentiation of the ilio-costalis and longissimus probably occurred in conjunction with the dorsal growth of the ilium.

9. The primitive longissimus was a broad, thick muscle which took origin on the dorsal surface of the ilium and the sacral rib. With the expansion of the limb muscles, the dorsal part of the iliac shaft turned over medially, carrying the longissimus with it and causing this muscle to become narrow and deep.

10. Primitively the ilio-costalis was a narrow muscle which took origin on the lateral surface of the ilium. As the dorsal part of the iliac blade folded inward, the ilio-costalis was

carried to the dorsal surface and eventually was isolated from the exterior surface of the ilium by a further expansion of this bone. The muscle retained its original insertions on the ribs but expanded medially, following the longissimus dorsi, to become a broad sheet of muscle.

11. The primitive longissimus cervico-capitis and ilio-costalis cervico-capitis were broad muscles forming a direct cranial extension of their dorsal equivalents. As the cervical ribs became shorter, these muscles migrated medially, becoming narrow. The ilio-costalis cervico-capitis eventually lost its connection with the ilio-costalis dorsi.

12. The heavy, tendinous interspinal muscles of *Eryops* were a means of support of an otherwise weak spinal column.

13. The tendinous character and thickness of the interspinal muscles of *Diadectes* and other cotylosaurs compensated in some degree for the weak support of the spinal column afforded by the short neural spines to which these muscles attached and the poor articulation between the centra. Other features serving the same purpose were the wide neural arches and zygapophyses, the hyposphenes and hypantra, the strong tendinous interarticulars, and the intervertebral ligament.

14. The large levator costae of *Diadectes* and *Dimetrodon* were important in the support and movement of the ribs of these animals.

15. The occipital muscles were well differentiated in forms as primitive as *Eryops* and *Diadectes*, and were essentially modern in their development.

16. The rectus capitis posterior is better developed in advanced forms than it was in primitive ones. In recent reptiles it is usually divided into two muscles, the rectus capitis posterior superficialis and rectus capitis posterior profundus.

17. The fact that the cervical muscles of various forms in the evolutionary series have inserted on different bones of the skull is of little significance in the development of the muscles. A change in area of insertion of the muscles, on the other hand, is important.

18. Among living reptiles, the condition of the back musculature of *Sphenodon* most closely approaches the pattern inferred for primitive forms. It appears to fall midway between the condition inferred in *Diadectes* and *Dimetrodon*.

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